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Chapter 9
Adaptive Diversification in Coevolutionary Systems

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Abstract Coevolution can trigger frequency-dependent selection by reciprocal effects on the fitness of involved species. Through directional and disruptive selection, coevolution can lead to rich evolutionary possibilities. It can be classified by major types of biotic interactions (mutualism and antagonism) or by the number of species involved (specific, diffuse and escape-and-radiate coevolution). Using two mainstream methods for studying the evolution of quantitative traits [adaptive dynamics (AD) based on canonical equations and evolutionary distribution (ED) based on trait diffusion], we examine three coevolutionary systems, including those driven by mutualistic and antagonistic interactions, as well as food webs. Results highlight the importance of trait-mediated competition, assortative cross-trophic interactions and consumption niche width (dietary width) on adaptive diversification in these coevolutionary systems. Interactions between two species can lead to diffuse and escape-and-radiate coevolution, making coevolutionary networks an ideal model for studying complex adaptive systems.

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9.1 Introduction

Evolutionary adaptation is traditionally viewed as a hill-climbing and niche-filling process in a static fitness landscape, and the potential diversification from such adaptation often occurs allopatrically along an environmental gradient or through the restriction of gene flows by geographical barriers. Consequently, the number of species that a local ecosystem can hold depends on the intensity of niche competition and the carrying capacity of the environment. Coevolution, in contrast, often

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triggers frequency-dependent selection where the evolutionary change in one species can lead to a reciprocal change in another species to balance their fitness. Such a dynamic fitness landscape then allows species to converge and diverge, respectively, through directional and disruptive selection, resulting in a wide variety of evolutionary possibilities.

The phenomenon of coevolution was first speculated by Darwin in 1862 and related to a moth with a 30-cm-long proboscis that pollinates an orchid of similar shape. The former was later discovered in 1903 to be the sphinx moth *Xanthopan morganii praedicta* and the latter, the Madagascan orchid *Angraecum sesquipedale*. The two coevolving species, as Darwin (1862) put it, 'might slowly become, either simultaneously or one after the other, modified and adapted in the most perfect manner, by the continued preservation of individuals presenting mutual and slightly favourable deviation of structure'. Coevolution can typically be classified according to the type of biotic interactions: largely mutualistic interactions (e.g. pollination and seed dispersal networks) and antagonistic interactions (e.g. predation and parasitism networks, as well as food webs).

Species maintain a mutualistic interaction by providing each other with benefits (fitness gains) as is the case of the Madagascan orchid and the sphinx moth. In this pollination syndrome, the moth pollinates the flower and in return is rewarded the sugar-rich nectar from the orchid. By changing the interacting functional traits through evolution (e.g. the proboscis of pollinators and the floral tube of flowers), mutualistic interactions can lead to intriguing coevolutionary games. Some long-standing mutualistic interactions can lead to the symbioses of both partners such as the symbiotic mycorrhizas formed in many plants with glomeromycete fungi. The fungus helps the plant obtain water and phosphates and is rewarded in turn with carbohydrates from the plant. To this end, some have argued that an organism is better understood as a compound system together with its symbionts (Gilbert et al. 2012), such as the extreme case in the evolution of mitochondria from purple bacteria and chloroplasts from cyanobacteria (Moran 2007). Maintaining a symbiotic or mutualistic relationship can be costly. As such, a major challenge is to unveil the protective mechanism that the involved partners have adopted for discerning and correcting the cheating behaviour which can be disastrous to the functioning of the system (Pellmyr and Leebens-Mack 1999).

Antagonistic interactions often occur through the mediation between the foraging traits of predators and the anti-foraging traits of their prey, such as between the speed of cheetahs and the agility of gazelles, between the fish stock and fishery policies (Landi et al. 2015) and between the toxicity of rough skinned newts (*Taricha granulosa*) and the resistance of garter snakes (*Thamnophis sirtalis*) (Hanifin et al. 2008). The drastic antagonistic warfare between plants and herbivores has resulted in the syntheses of diverse secondary compounds by plants as a defence mechanism against herbivores (Fraenkel 1959). Coevolution via antagonistic interactions can also lead to interesting phenomena of aposematism and mimicry (Mallet 2010), such as the coloration in the poison dart frog *Ranitomeya imitator* (Chouteau and Angers 2012). Again, the key to elucidating an antagonistic

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interaction is to identify the interacting traits that affect the predator's energy intake and the prey's survival.

Antagonism is also typical between the arms race of hosts and their parasites or pathogens. Reed warblers distinguish artificial eggs closely resembling their own, while brood parasitic cuckoos *Cuculus canorus* produce eggs that are increasingly difficult for host warblers to recognize (Rothstein and Robinson 1998). Examples of host-parasite coevolution abound in many infectious diseases. Planktonic crustacean *Daphnia magna* can control the infectivity of the parasitic bacterium *Pasteuria ramose* while facing an ever-increasing virulence of the parasite (Decaestecker et al. 2007). Of course, the coevolution between the host and pathogens does not necessarily lead to an ever higher level of virulence as many pathogens require the well-being of their hosts for vertical transmission. The weakening virulence of human immunodeficiency virus (HIV) can be considered an example of reduced virulence from the antagonistic coevolution between the virulence and the host's immunity (Payne et al. 2014).

Although coevolution, by definition, involves a specific pair of species, it can be expanded to include multiple interacting species in interacting guilds or lineages (Futuyma and Slatkin 1983; Thompson 1994; Futuyma 2013). As aforementioned, two species in *specific coevolution* are engaging an evolutionary arms race through the interaction of their functional traits that affect each other's fitness. Such specific coevolution can typically lead to matched traits through convergence evolution in mutualistic systems and evolutionary cycles known as the Red Queen dynamics in antagonistic systems. In *diffuse coevolution*, several species from a functional guild affect each other's fitness by their own evolutionary changes (Zhang et al. 2011). In *escape-and-radiate coevolution*, the interaction between species enables one or both species to radiate into a diverse clade (Hui and McGeoch 2006; Rezende et al. 2007; Minoarivelo et al. 2014). Importantly, the coevolution between two species could lead to diffusive and then escape-and-radiate coevolution, through the process of adaptive diversification triggered by repeatedly occurring disruptive selection in the system (Brännström et al. 2011). Such adaptive diversification from coevolution is the concern here.

To date, direct examples of adaptive diversification from coevolution have been rare. One such case has been detected in the Darwin's race between a long-proboscid fly, *Moegistorhynchus longirostris*, of the Nemestinidae family and a long-tubed iris, *Lapeirousia anceps*, of the Iridaceae family (Fig. 9.1). In this arms race, effective feeding occurs when proboscis length exceeds floral tube length because the pollinator is then able to drain all the nectar from the flower; in contrast, effective pollination occurs when floral tube length exceeds proboscis length because this ensures sufficient contact with the stigma and anthers near the entrance of the floral tube (Pauw et al. 2009). These two coevolving traits thus impose reciprocal directional selection on each other, leading to an escalating arms race. Imbalanced costs to trait elongation, constrained by physiological constraints and related to environmental variation, trigger the divergent selection and the trait dimorphism in the high-cost species (specifically in some iris populations; Zhang et al. 2013).

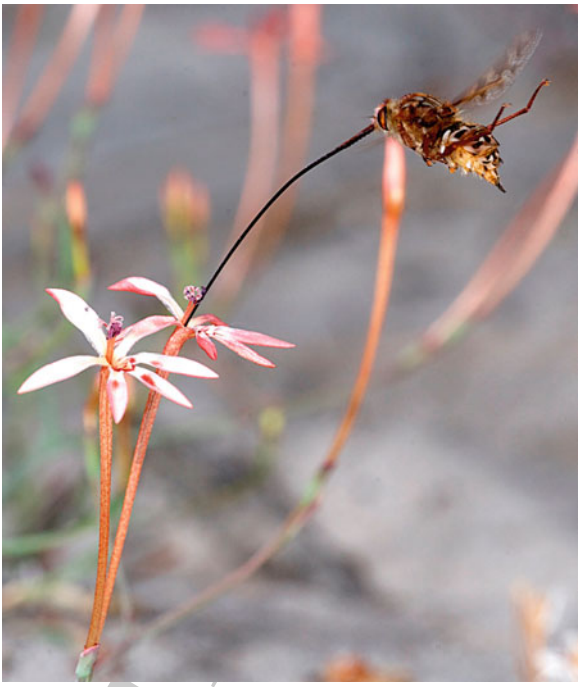

Fig. 9.1 Darwin's race between the long-proboscid fly, *Moegistorhynchus longirostris*, and the long-tubed iris, *Lapeirousia anceps*, in South Africa. (Photograph courtesy of A. Pauw)

Phylogenetic evidence of adaptive diversification from escape-and-radiate coevolution is common, suggesting coevolution also a potential source of clade diversification. The mutualistic interaction of seed dispersal by ants, known as myrmecochory, could have promoted diversification in flowering plants (Lengyel et al. 2009). Pollination syndrome between insects and flowers could explain why angiosperms of flowering plants are more diverse than gymnosperms. Escape-and-radiate coevolution could also be common between plants and herbivores, such as between the leaf beetles Blepharida and their host trees Bursera (Becerra and Venable 1999) and between endosymbiotic bacteria *Buchnera aphidicola* and aphids (Moran and Baumann 1994). Moreover, when multiple species are closely involved in a community, they often form an adaptive coevolutionary network (Zhang et al. 2011), with a mixture of mutualistic and antagonistic interactions affecting each other's fitness. For instance, leaf-cutter ants nourish the actinomycete bacteria *Pseudonocardia* by their gland secretions and use the antibiotic produced by the bacteria to inhibit the growth of the unpalatable fungi Escovopsis that competes with their food fungus Lepiotaceae in their fungal garden (Futuyma 2013).

All these clues have suggested that coevolution can potentially lead to rich evolutionary trajectories via frequency-dependent selection, in particular the possibility of diversification and polymorphism via evolutionary branching by disruptive selection in the system. These clues have further triggered abundant theoretical studies, attempting to understand how these trait-mediated interactions

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in coevolutionary systems trigger disruptive selection and adaptive diversification (Doebeli and Dieckmann 2000). Using phylogenies as the record of evolutionary history, studies have shown that coevolution could explain, to a certain degree, contemporary structures of many ecological networks (Rezende et al. 2007; Minoarivelo et al. 2014). Here, we use two numerical approaches of evolutionary invasion analysis, known as AD and ED, to explore the patterns and conditions of adaptive diversification and evolutionary branching in generic models of mutualism, antagonism and food webs. Specifically, we explore under what conditions a pair of interacting species can potentially trigger disruptive selection and diversify through specific, diffuse and even escape-and-radiate coevolution.

9.2 Evolutionary Invasion Analysis

Evolutionary trajectory is traditionally regarded as the process of organisms attempting to maximize their fitness via optimizing its life-history strategies (or loosely defined as traits). Such a perspective involves two assumptions. First, there is a fitness measure that can be maximized in the attainable trait set. Second, this optimal trait can be reached, from the current stand, through incremental evolutionary changes. The first assumption leads to the definition of the evolutionarily stable strategy (ESS): there exists a trait that has competitive advantage over all other attainable traits; in other words, it can resist the invasion of all other traits. The second assumption refers to the convergence (asymptotic) stability of this optimal trait; that is, a trait close to the optimal trait can be invaded/replaced by a trait even closer to the optimal trait through directional selection. A convergence stable ESS is called a continuously stable strategy (CSS). Evolutionary invasion analysis is a set of quantitative techniques designed to address these two assumptions: conditions for the existence of an ESS and for a rare mutant trait to invade a resident population (Otta and Day 2007). Notably, the invading trait normally is considered not far from the resident one; that is, we are looking for a local CSS, strategies that are convergence stable and cannot be invaded by local traits. However, with the onslaught of global environmental changes, many non-indigenous species or genotypes are constantly being introduced to native ecosystems, suggesting an increasing relevance of searching for the global CSS in an evolutionary system. In the following, we first introduce two approaches for evolutionary invasion analysis and then apply these approaches to coevolutionary models of mutualism, antagonism and food webs

9.2.1 Adaptive Dynamics

Adaptive dynamics (AD) is a powerful analytical tool for studying the evolution of quantitative traits or phenotypic characters, developed in the 1990s by game

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theorists (e.g. Nowak and Sigmund 1990), population geneticists (e.g. Abrams et al. 1993) and theoretical ecologists (e.g. Metz et al. 1992; Dieckmann and Law 1996). It studies evolutionary changes induced by rare and small mutations when fitness is density or frequency dependent (Waxman and Gavrilets 2005). As individuals interact within a community, their fitness not only depends on their own traits but also depends on the frequency or density of different traits among individuals. The evolution of traits can be evaluated by examining the survival of rare mutants in a community dominated by resident populations at their stable equilibriums. To this end, the *canonical equation* of AD describes the evolution of traits under directional selection through the continuous invasion of rare mutants into resident populations.

We illustrate here the standard procedure of using AD in a resource competition model. For a given set of n traits, changes in population densities $u_i (i = 1, 2, \ldots, n)$ are described by the Lotka–Volterra model,

$$\frac{\mathrm{d}u_i}{\mathrm{d}t} = ru_i\left(1 - \frac{\sum_l \alpha(x_i, x_l)u_l}{k(x_i)}\right), \tag{9.1}$$

where r is the intrinsic population growth rate, $k(x_i)$ the trait-dependent carrying capacity and $\alpha(x_i, x_k)$ the competition strength between individuals with trait value x_i and x_k. Because mutations only occur at a low rate, the population densities are considered to be already at their equilibriums when a mutation happens. In this regard, we need to distinguish two different timescales in the concept of AD: a slow evolutionary timescale (including the slow trait shift by directional selection and the even slower evolutionary branching by disruptive selection) and a fast ecological timescale. Let x' be the trait value of a rare mutant, $x = (x_1, x_2, \ldots, x_n)$ the resident traits and u_i^* the population density at equilibrium. The invasion fitness of the mutant can be described as its per capita growth rate when setting its initial density to be negligible:$f(x, x') = r(1 - \sum_l \alpha(x', x_l)u_l^*/k(x'))$. The selection gradient of population i, $g(x_i) = \partial f(x, x')/\partial x'|_{x'=x_i}$, determines the speed of directional selection. The evolutionary dynamics of trait x_i can be depicted by the *canonical equation* as being proportional to the selection gradient (Dieckmann and Law 1996), $\dot{x}_i = \varepsilon \cdot u_i^* g(x_i)$, where ε is a parameter related to the rate and variation of mutation. If the directional selection pushes the traits to become unfeasible (i.e. the population density at equilibrium becomes equals or less than zero), it is termed an evolutionary suicide (Gyllenberg et al. 2002).

Let x_i^* indicate the trait when the selection gradients of all resident traits disappear, termed an evolutionary singularity. The singularity is convergence stable if all eigenvalues of the Jacobian of the canonical equations have negative real parts (Doebeli and Dieckmann 2000); in this case, $\partial g/\partial x_i|_{x_i=x_i^*} < 0$. The singularity represents a fitness minimum, an indication of disruptive selection, if the curvature of fitness landscape is greater than zero, $\partial^2 f/\partial x'^2|_{x'=x_i^*} > 0$, allowing traits other than the singularity to invade (Geritz et al. 1998); intuitively, the curvature is also a measure of the strength of disruptive selection. To have an evolutionary branching,

not only the singularity needs to be a fitness minimum and under disruptive selection, but also the two morphs emerged from the evolutionary branching need to be protected (Geritz et al. 1998); that is, the two morphs (x' and x'') can invade each other: $(\partial^2 f/\partial x'^2 + \partial^2 f/\partial x''^2)|_{x'=x''=x_i^*} > 0$. If the singularity represents a fitness maximum (i.e. an ESS) and convergence stable (i.e. a CSS) but the dimorphism cannot be protected, it is called an evolutionary trap (Zhang et al. 2013).

9.2.2 Evolutionary Distribution

For simplicity, common approaches of evolutionary invasion analysis, such as AD, often ignore the variation of traits and only consider the evolution of average traits (Dieckmann and Law 1996; Champagnat et al. 2001, but see Barton and Turelli 1987; Sasaki and Dieckmann 2011). However, studying only the evolution of average traits may overlook many important ecological and evolutionary features. Bolnick et al. (2011) have identified different mechanisms by which trait diversity can affect the outcome of ecological interactions. Ignoring trait variation can also lead to an underestimation of the spreading velocity in many invasive species (Ramanantoanina et al. 2014). Furthermore, numerical analyses of mean traits often rely on the separation of ecological and evolutionary timescales. This assumption is inconsistent with recent observations that ecological and evolutionary processes can occur at similar timescales (Yoshida et al. 2003; Jones et al. 2009).

Following the initial proposition of Levin and Segel (1985), Cohen (2003) coined the term of ED that studies the evolution of trait distribution in a continuous space. Cohen (2009) further suggested that considering only the mean phenotypic trait may mislead studies to traits that might not be adopted by any individuals in real populations. The concept of evolutionary distribution (ED) was initiated by Levin and Segel (1985), though the term was coined by Cohen (2003). ED studies the evolution of trait distributions in a continuous space. Reaction diffusion models are derived from ecological and evolutionary principles. While the reaction term is used to capture ecological processes such as competition and predation, the diffusion term represents the process of mutation that allows the phenotypic traits to drift on the trait space.

Using the framework of ED, the eco-evolutionary dynamics of species undergoing resource competition can be modelled by (Doebeli and Ispolatov 2010),

$$\frac{\partial u}{\partial t} = ru\left(1 - \frac{\int \alpha(x,y)u(y,t)\mathrm{d}y}{k(x)}\right) + \eta\frac{\partial^2 u}{\partial x^2}, \tag{9.2}$$

where η is the trait diffusion rate. A *morph* is defined as a trait value where the ED reaches a local maximum of frequency, and the diversity can be quantified by the number of *morphs,* i.e. the number of local maxima as well as the variance of the trait distribution around each morph (Cohen 2009; Doebeli and Ispolatov 2010).

Stable ED represents a set of ESS because all possible mutants are included in the ED (Cohen 2009). However, the study of stable ED can also be more complicated as the stability theory of partial differential equations, especially of nonlinear systems, is far from complete. Here, all initial conditions for the ED models correspond to a Dirac mass at the peak of resource distribution. A branching event is identified numerically when a local maximum emerges beside the previous one, or two local maxima appear around the previous one. To minimize the risk of a false branching (numerical fluctuations can be mistakenly taken as local maxima), branching is detected only every 20 time steps, and further fine-scale fluctuations are removed by the moving average algorithm.

9.3 Mutualistic Coevolution

9.3.1 Modelling Mutualistic Coevolution

Since Darwin's coevolutionary hypothesis between flower traits and the features of their pollinators, some patterns of mutualistic communities have been attributed to coevolution. For instance, the yucca moth (*Tegeticula synthetica*) is the only pollinator of the Joshua tree (*Yucca brevifolia*), while the seed of Joshua tree is the only food source for the yucca moth. The speciation in the moth has resulted in the radiation of the flower shape in Joshua trees. However, as species in a community are simultaneously under different and often conflicting selection pressures (such as also from predation and intra-specific competition), mutualism may not be the main driver of adaptive diversification (Raimumdo et al. 2014).

To study the role played by mutualistic interactions in generating diversification, we expand the Lotka–Volterra model with a Holling (1959) type II functional response. The population dynamics is governed by the demography, including intrinsic population growth and density dependence, and the additional contribution from the mutualistic interaction. For the AD approach, let there be n functional morphs of animals and m functional morphs of plants. Each functional morph, indexed by i for animals and j for plants, is characterized by its population density u_i and v_j, respectively. In a pollination system, the functional trait of each morph could represent the proboscis length of the pollinator, or the length of pollen tube of the flowering plant. We denote the trait of animal morph i by x_i and the trait of plant morph j by y_j. The population dynamics of the AD system thus is given by,

$$\begin{aligned}\frac{\mathrm{d}u_i}{dt} &= r' u_i \left(1 - \frac{\sum_l \alpha'_{il} u_l}{k_1(x_i)}\right) + \frac{u_i \sum_l \gamma_{il} \omega'_{il} v_l}{1 + h \sum_l \omega'_{il} v_l} \\ \frac{\mathrm{d}v_j}{dt} &= r'' v_j \left(1 - \frac{\sum_l \alpha''_{jl} v_l}{k_2(y_j)}\right) + \frac{v_j \sum \gamma_{lj} \omega''_{lj} u_l}{1 + h \sum_l \omega''_{lj} u_l}\end{aligned} \tag{9.3}$$

where h is the handling time. The equivalent ED model for the coevolution of mutualistic species can be written as the following:

$$\begin{aligned}\frac{\partial u}{\partial t} &= r'u\left(1-\frac{\int\alpha'(z)u(x-z)\mathrm{d}z}{k_1(x)}\right)\\ &\quad+\frac{u\int\gamma(z)\omega'(z)v(z)\mathrm{d}z}{1+h\int\omega'(z')v(z')\mathrm{d}z'}+\eta\frac{\partial^2 u}{\partial x^2}\\ \frac{\partial v}{\partial t} &= r''v\left(1-\frac{\int\alpha''(z)v(y-z)\mathrm{d}z}{k_2(y)}\right)\\ &\quad+\frac{v\int\gamma(z)\omega''(z)u(z)\mathrm{d}z}{1+h\int\omega''(z')u(z')\mathrm{d}z'}+\eta\frac{\partial^2 v}{\partial y^2}\end{aligned} \tag{9.4}$$

Specifically, we assign the trait-dependent carrying capacity, $k_1(x_i) = K_1N(x^{\max}, \delta_1, x_i)$, where $N(\mu, \sigma, x)$ is a Gaussian density function at x with the mean μ and standard deviation σ, and K_1 is the carrying capacity for optimal trait $x^{\max}$, and the standard deviation of the Gaussian function, δ_1, represents the resource niche width accessible to the animals. The carrying capacity for plants, $k_2(y_j)$, is similarly defined. The intra-trophic competition kernels (α' and α") are set to let more similar morphs suffer stronger competition, (Bürger et al. 2006; Doebeli and Dieckmann 2000; Raimumdo et al. 2014): $\alpha'_{il} = N(x_i, \sigma_1, x_l)$ or $\alpha'(z) = N(x, \sigma_1, z)$, where σ_1 controls the width of the competition kernel. The cross-trophic mutualistic benefit, $\gamma_{ij} = \lambda N(x_i, \sigma_m, y_j)$ or $\gamma(z) = \lambda N(x, \sigma_m, z)$, reflects the assumption that matching traits bring high profit to each other, where λ is a parameter controlling the magnitude of the mutualistic support, and the parameter σ_m controls the tolerance level of successful interactions to the trait difference of involved traits (Nuismer et al. 2010). The interaction preference (ω'_{ij} and ω''_{ij}) of the two morphs determines the possibility of interaction after an encounter and is assumed following the adaptive foraging strategy, depending on both the benefit and abundance of the involved morphs (Doebeli and Dieckmann 2000): $\omega'_{ij} = \gamma_{ij}\sum_l u_l / \sum_l(\gamma_{lj}u_l)$, where the summation term $\sum_l u_l$ in the numerator is for normalization, or $\omega'(z) = \gamma(z)\int u(z')dz / \int\gamma(z'')u(z'')dz''$. The two approaches, AD and ED, were numerically solved with an initially monomorphic population, with a unit density for both plants and animals. Under the AD approach, the three conditions for evolutionary branching are examined once the system reaches its singularity.

9.3.2 *Diversification by Mutualism*

We focused on three key parameters in the system and examined their effects on the evolutionary dynamics, including the standard deviations of competition (σ_1 and σ_2) and the tolerance to trait difference (σ_m). The widths of carrying capacity (δ_1 and δ_2) are kept equal for simplicity (=1.65). Other parameters were fixed throughout the

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chapter unless specified ($r' = r'' = 1; h = 0.1; \lambda = 0.25; x^{\max} = 3; K_1 = 300; y^{\max} = 2; K_2 = 400$). As illustrated in Fig. 9.2, mutualistic interactions between a monomorphic animal population and a monomorphic plant population, inserted in a resource competition model (Eqs. 9.3 and 9.4), can trigger disruptive selection and lead to diffuse and even escape-and-radiate coevolution.

Evolutionary branching is more likely to happen for stronger tolerance to trait difference (larger σ_m) and narrower competition kernel (smaller σ_1 and σ_2) (Fig. 9.3a). Adaptive diversification only happens to one species when its competition kernel is narrower than the competition kernel of its mutualistic partner species. Narrow competition kernel suggests an intense trait-specific competition, i.e. strong negative frequency dependence, which is a common condition for diversification (Day and Young 2004; Doebeli and Ispalatov ~~2011~~).

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When the tolerance to trait difference is low (small σ_m), the trait value of a morph needs to become more similar to the trait value of its interacting morph to take advantage of the benefit from the mutualistic interaction (Fig. 9.3b), leading to matched traits. It is worth noting that such matched traits from low tolerance are often not the end point of coevolution, as evolutionary branching normally occurs after the trait matching. In contrast, when species have strong tolerance to trait difference (large σ_m), as in many generalists, the reciprocal selection for trait convergence is not strong, leading to bias in trait matching, or mismatched traits (Fig. 9.3b). In addition, patterns of trait matching or mismatching, as depicted by the trait value ratio in Fig. 9.3, are predominantly governed by the mutualistic term in the model and nearly independent of competition (i.e. insensitive to σ_1 and σ_2).

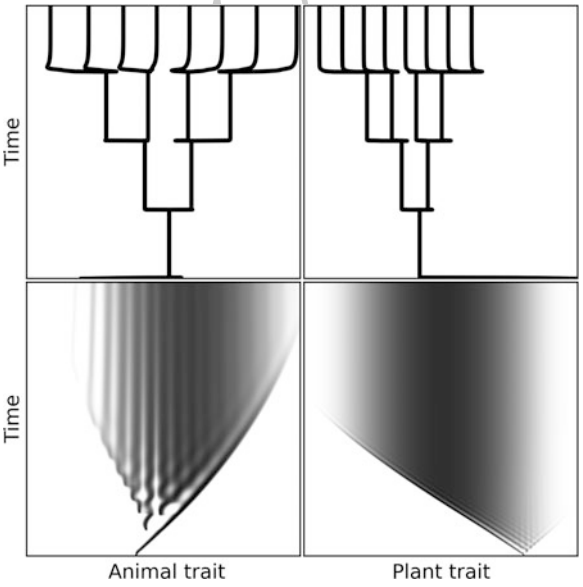

Fig. 9.2 Adaptive diversification triggered by mutualistic interactions. Parameters: $\sigma_1 = 0.14$; $\sigma_2 = 0.08$; $\sigma_m = 1$. *Top panel* is generated by the adaptive dynamics method; *bottom panel* is generated by the evolutionary distribution method

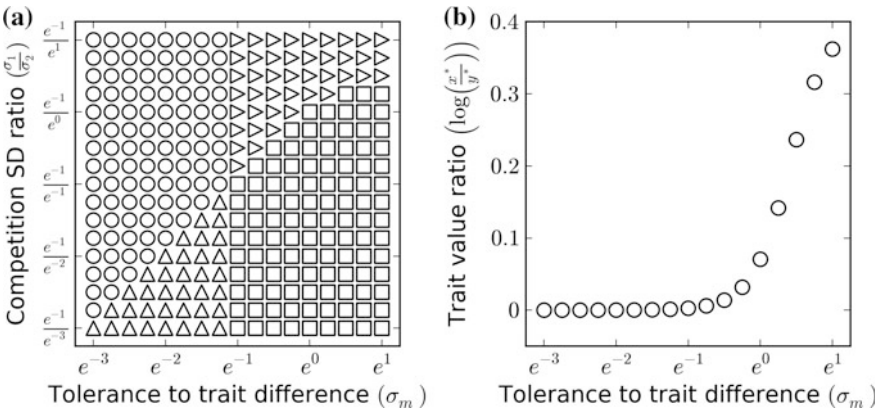

Fig. 9.3 Effects of competition kernel and tolerance to trait difference on evolutionary branching in mutualistic systems. **a** Evolutionary branching scenarios with respect to the tolerance to trait difference (σ_m) and competition standard deviations (σ_1 and σ_2) for mutualistic interactions. *Squares* represent branching in both animals and plants; *right-facing triangles* represent branching only in animals; *up-right triangles* represent branching only in plants; *circles* represent no branching. **b** The trait value ratio (animal over plant) at the first branching point as a function of the tolerance to trait difference. Both figures were obtained using the adaptive dynamics method

9.4 Antagonistic Coevolution

9.4.1 Modelling Antagonistic Coevolution

Many laboratory experiments have been conducted for observing the effect of antagonistic interactions on the diversification in coevolutionary systems. Specifically, the coevolution between hosts and their perspective parasites has been extensively studied. Results suggest that although hosts often develop resistances against their parasites, this often triggers the adaptive diversification in the parasites which in turn diversifies the resistance strategies of hosts, commonly termed as the arms race dynamics (Marston et al. 2012). In what follows, we once again make use of the Lotka–Volterra model for depicting the dynamics of predator densities (u_i) and prey densities (v_i):

$$\begin{aligned}\frac{\mathrm{d}u_i}{\mathrm{d}t} &= -r' u_i \left(1 + \frac{\sum_l \alpha'_{il} u_l}{k_1(x_i)}\right) + \frac{\lambda u_i \sum_l a\gamma_{il} v_l}{1 + h\sum_l a\gamma_{il} v_l} \\ \frac{\mathrm{d}v_j}{\mathrm{d}t} &= r'' v_j \left(1 - \frac{\sum_l \alpha''_{jl} v_l}{k_2(y_j)}\right) - \frac{v_j \sum_l a\gamma_{lj} u_l}{1 + h\sum_l a\gamma_{il} v_l}\end{aligned} \tag{9.5}$$

where functions for intra-trophic competition are similar to those in the mutualistic model. The attack rate of the prey j with trait y_j by the predator i with trait x_i is governed by a Gaussian function of trait difference, $a\gamma_{ij} = aN(x_i\text{-}\mu_p, \sigma_p, y_j)$. The

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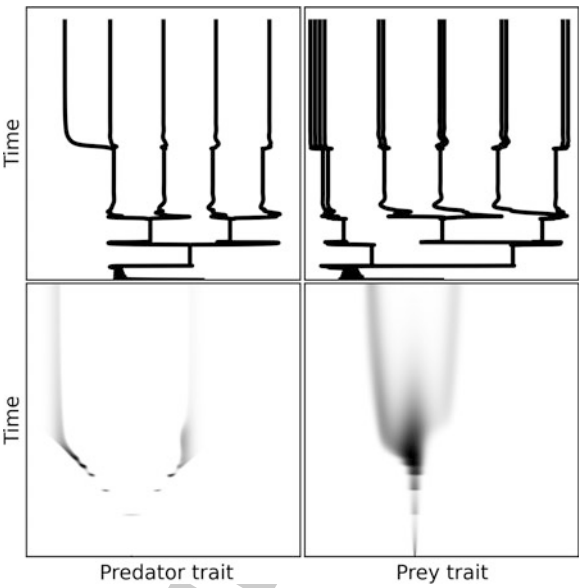

Fig. 9.4 Adaptive diversification triggered by antagonistic interactions. Parameters: $\sigma_1 = \sigma_2 = e^{-1}; \sigma_p = e^{0.25}$. *Top panel* is generated by the adaptive dynamics method; *bottom panel* by the evolutionary distribution method

attack rate is maximal when the prey trait value (y_j) is the predator trait value (x_i) minus μ_p. As above, the evolutionary dynamics of the traits can be derived from the canonical equation of the AD. Of course, we can also model the evolutionary dynamics of the predator–prey interactions using the ED framework.

9.4.2 Diversification by Antagonism

We focused here on the effects of competition kernels (σ_1 and σ_2) on adaptive diversification. Another key parameter that can affect diversification is the dietary width of predators (σ_p) which will be explored in the next section on food webs. The widths of carrying capacity were kept equal for simplicity ($\delta_1 = \delta_2 = 2$). Other parameters were fixed to be the same as in the model for mutualism, except that $r' = 0.01; \lambda = 0.3; a = 0.5; \mu_p = 1/3$. First, it is clear that the antagonistic interaction can lead to disruptive selection and evolutionary branching, using both methods (Fig. 9.4). Evolutionary branching is more likely to occur in predators, especially when the competition kernel of predators (σ_1) is relatively high ($>e$) where the branching happens exclusively to predators (Fig. 9.5a). In other words, prey cannot diversify if the competitive interference between predators is strong (large σ_1). Strong competitive interference between predators also generates larger foraging traits in predators than the anti-predation traits of prey at the first branching event (Fig. 9.5b). Moreover, when the competition between predators is strong but that between prey is weak (the bottom right corner in Fig. 9.5), the system becomes unstable, suggesting that the increased mortality due to

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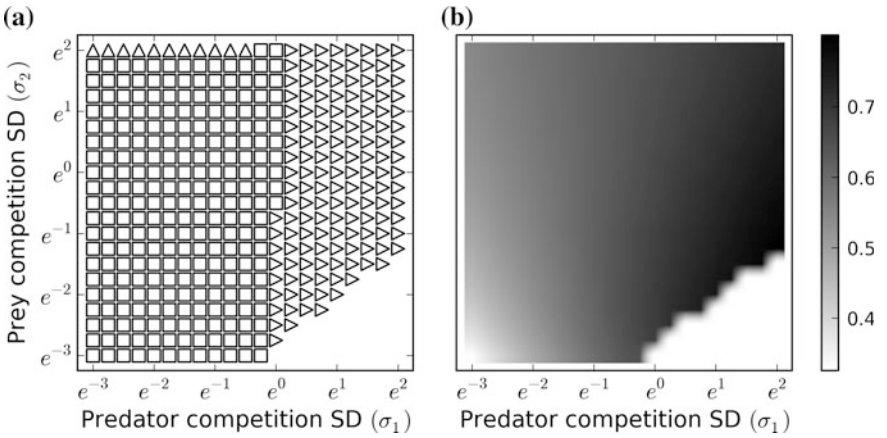

Fig. 9.5 Effects of competition kernels on evolutionary branching in predator–prey systems. **a** Evolutionary branching scenarios with respect to the competition kernel of the predator and prey. *Squares* represent branching in both predators and prey; *right-facing triangles* represent branching only in predators; *up-right triangles* represent branching only in the prey. The *empty area* represents the extinction of either species. **b** The trait value ratio (predator over prey) at the first branching point. Both figures were obtained using the adaptive dynamics method

intensive intra-trophic competition has exceeded the capacity that the cross-trophic energy flow can support, producing a zone of evolutionary suicide if convergence occurs.

9.5 Food Webs

9.5.1 Modelling Food Webs

Food webs exhibit more complex dynamics as they encompass a variety of interactions such as antagonism and competition across multiple trophic levels. For such a complex system, mathematical models of coevolution can provide insights as to the conditions that foster diversification within and cross-trophic levels (Cattin et al. 2004; Loeuille and Loreau 2005; Brännström et al. 2011, 2012). In particular, Brännström et al. (2011) have explored the role of body size as the key functional trait in initiating, structuring and maintaining food web biodiversity. Here, we use a similar model but with a type II functional response to explore the conditions that promote diversification in a food web, with specific emphasis on the role of the consumption kernel (explained below).

Consider a basal autotrophic resource ($i = 0$) and n heterotrophic morphs with population densities (u_i) such that each morph is associated with its average body size s_i. While defining the trait value of each morph as the body size relative to the autotroph, $x_i = \ln(s_i/s_0)$, we can describe the dynamics of heterotrophic morphs by the following Lotka–Volterra equations:

$$\frac{\mathrm{d}u_i}{\mathrm{d}t} = -d_i u_i + \sum_{j=0}^{n} \lambda \frac{s_j}{s_i} \frac{a\gamma_{ij} u_j u_i}{1 + \sum_{k=0}^{n} h_{ik} a \gamma_{ik} u_k} - \sum_{j=1}^{n} \frac{a\gamma_{ji} u_i u_j}{1 + \sum_{k=0}^{n} h_{jk} a \gamma_{jk} u_k} - \sum_{j=1}^{n} \frac{1}{k_1} \alpha_{ij} u_i u_j \quad , \tag{9.6}$$

where the intrinsic death rate $d_i = \exp(-qx_i)$, following Brännström et al.(2011); a is the attack rate; α_{ij} describes the mortality rate as a result of interference competition between morphs i and j, while $1/k_1$ defines the intensity of competition. Here, the competition kernel α_{ij} follows a Gaussian distribution as defined above. The consumption kernel γ_{ij} describes the probability of a morph i individual successfully hunting and consuming a morph j individual after the encounter and is assumed to follow a normal distribution, $\gamma_{ij} = N\left(\mu, \sigma_p, x_i - x_j\right)$, where μ defines the optimal consumer to resource body size ratio at which the consumer can make the most successful attacks, and σ_p describes the dietary niche width (i.e. the standard deviation of the consumption kernel). Conversion parameter λ is the fraction of captured resources that a consumer uses for its reproduction. The handling time h_{ij} is the time a consumer morph i spends handling one individual of morph j; following Kalinkat et al. (2013), we let $h_{ij} = h_0 s_j s_i^{-3/4}$. The demographic dynamics of the autotrophic morph can be described as follows:

$$\frac{du_0}{dt} = ru_0\left(1 - \frac{u_0}{k_2}\right) - \sum_{j=1}^{n} \frac{a\gamma_{j0} u_0 u_j}{1 + \sum_{k=0}^{n} h_{jk} a \gamma_{jk} u_k}, \tag{9.7}$$

where r is the intrinsic growth rate of the autotrophic resource; k_2 is the carrying capacity such that r/k_2 depicts the strength of density dependence in the resource.

To study the emergence of a food web using the ED framework, we consider the integro-partial differential equation for the heterotrophic morphs:

$$\begin{aligned} \frac{\partial u}{\partial t} &= -\mathrm{d}(x)u - \frac{1}{k_1}\int_{\mathrm{H}} \alpha(y)u(x-y)\mathrm{d}y \\ &\quad - u\int_{\mathrm{H}} \frac{\gamma(y,x)u(y)}{1 + \int_{\mathrm{A}\cup\mathrm{H}} h(y,z)\gamma(y,z)u(z)\mathrm{d}z}\mathrm{d}y \\ &\quad + u\int_{\mathrm{A}\cup\mathrm{H}} (\lambda e^{y-x}) \frac{\gamma(x,y)u(y)}{1 + \int_{\mathrm{A}\cup\mathrm{H}} h(x,z)\gamma(x,z)u(z)\mathrm{d}z}\mathrm{d}y + \eta\frac{\partial^2 u}{\partial x^2} \\ \frac{\mathrm{d}u(0,t)}{\mathrm{d}t} &= r\left(1 - \frac{u(0,t)}{k_2}\right) - u(0,t)\int_{\mathrm{H}} \frac{\gamma(y,0)u(y)}{1 + \int_{\mathrm{A}\cup\mathrm{H}} h(y,z)\gamma(y,z)u(z)\mathrm{d}z}\mathrm{d}y \end{aligned} \tag{9.8}$$

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The first term on the right-hand side of the heterotrophic dynamics is the body-size-dependent intrinsic death rate. The second term captures the interspecific competition. The third term models the loss of biomass due to predation. The fourth term represents captured biomass used for reproduction. The fifth term depicts the trait diffusion. Subscript H indicates that the integration is performed over the heterotrophic morphs only, while subscript A U H represents that the integration is performed over both the heterotrophic and autotrophic morphs. The dynamics of autotrophic resource (the second equation) is assumed to follow a logistic growth in the absence of the heterotrophic morphs, with additional mortality of the autotrophic resource caused by predation by all heterotrophic morphs.

9.5.2 Diversification in Food Webs

In this section, we investigate the extent to which the dietary niche width of predators, depicted by the standard deviation of consumption kernel, σ_p, influences the first evolutionary branching event during the emergence of a food web. For all simulations, we set the initial density of one for both the autotrophic and heterotrophic morphs, with relative trait values 0 and 3, respectively. The top predator (largest trait value) gradually increases its body size, while the body size gap between the top predator and the autotroph is gradually filled up by meso-predators (Fig. 9.6). With the elapse of time, the morph richness is increasing, but the total biomass declines.

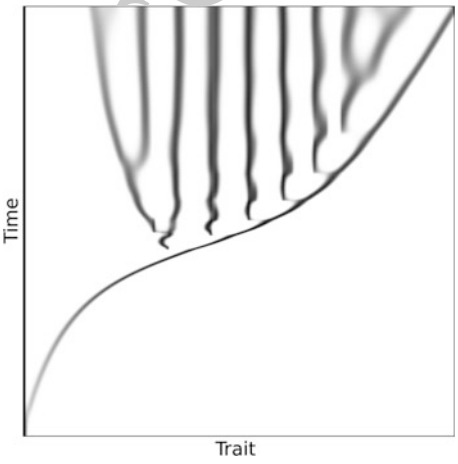

Fig. 9.6 Emergence of a food web from a single heterotrophic morph, obtained by using the evolutionary distribution method. Parameters: $r = 10, \lambda = 0.3, h_0 = 0.01, \eta = 0.001, q = 0.25, \sigma = 0.6$ (competition kernel), $a = 10, \mu = 3, \sigma_p = 1.5, s_0 = 1, k_1 = 300$ and $k_2 = 400$.

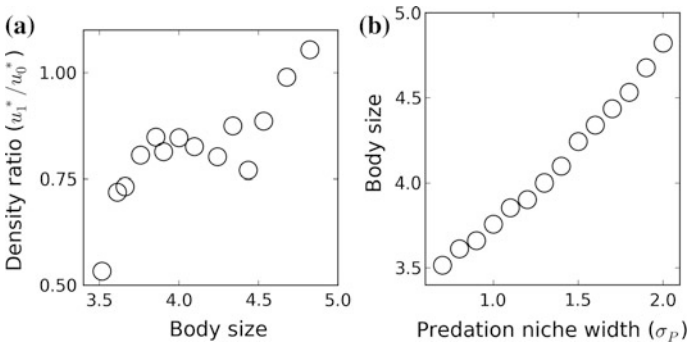

Fig. 9.7 Relationships between body size, density ratio and predation niche width at the first branching point in a food web. **a** Density ratio with respect to heterotroph body size at the first branching point. **b** Heterotroph body size as a function of the predation niche width. Parameters are the same as in Fig. 9.6

The strength of disruptive selection, measured by the curvature of fitness landscape at the singularity, increases with the increase of dietary width (σ_p) and the decrease of competition strength. This suggests that diversification, at least the first evolutionary branching, is easier in communities with more generalists than specialists. Importantly, parameters that foster the first evolutionary branching are not necessarily suitable for biodiversity maintenance (Brännström et al. 2011). Although many laboratory experiments have been designed to determine factors that favour the initial diversification (Buckling and Rainey 2002; Friesen et al. 2004; Nosil and Crespi 2006), more research is needed to understand how diversity is maintained along the evolutionary trajectory. Other factors may play an increasingly critical role for biodiversity maintenance with the increase of species richness but have only trivial effects when the system is species poor.

There is an overall positive relationship between the ratio of heterotroph to autotroph density and the heterotroph body size at the first singularity (Fig. 9.7a), with a local peak when the heterotrophy is at the optimal size for predation ($s_1 = 4$). The wider the predation niche (i.e. a diverse diet with large σ_p), the larger the body size of the heterotroph can become (Fig. 9.7b). Moreover, with the increase of dietary width, the body size ratio between adjacent morphs declines, and the food chains become longer as the mean predator–prey body size ratios decline (Jennings and Warr 2003). This is also true here since an increase in the standard deviation of the consumption kernel (σ_p) increases the strength of disruptive selection and hence supports high trophic levels. Since there is a strong correlation between body size and trophic level (Loeuille and Loreau 2005), a generalist top predator often has a larger body size than a specialist.

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9.6 Conclusion: Complex Adaptive Networks

Coevolution is a major source of adaptive diversification. Mutualistic and antagonistic interactions between species can strongly affect each other's fitness and trigger frequency-dependent selection which is essential for both evolutionary branching and diversity maintenance (Genieys et al. 2006; Doebeli and Ispolatov 2010; Biktashev 2014). As a species often has multiple functions in a community, e.g. as prey, predator, pollinator, etc., whether a specific biotic interaction drives adaptive diversification is often context based (Raimumdo et al. 2014). Resource competition has been shown to trigger niche-filling diversification, with a narrower competition kernel supporting easier diversification and higher species richness. Intra-trophic competition plays the same role in mutualistic and antagonistic coevolution, with narrower competition kernel (weaker trait-specific competition) more easily triggering disruptive selection and evolutionary branching.

A newly discovered factor in coevolution is the cross-trophic interaction, between flowers and pollinators and between predators and prey. Such bipartite interactions form a divide between the two functional groups. In mutualistic systems, adaptive diversification only happens to the group with a narrower competition kernel, indicating stronger negative frequency dependence (Day and Young 2004; Doebeli and Ispolatov 2011). Low tolerance to cross-trophic trait difference (σ_p) leads to matched traits but could then lead to diversification when competition is relatively strong. High tolerance as in many generalists often leads to bias between interacting traits. Strong cross-trophic interactions often lead to convergence evolution towards an ESS, while species involving weak cross-trophic interactions behave independently as resource competition within its own functional group. Mutualistic interactions can trigger diversification when the cross-trophic interaction is moderate so that asymmetric fitness between the two groups often triggers the diversification in the less fit group.

The two functional groups in antagonistic systems are not symmetrical as in mutualistic systems. Consequently, predators are more susceptible to disruptive selection and diversification, although competition within each group also plays a role in adaptive diversification. Food webs, a more generic antagonistic system than the bipartite network, behave rather similarly. Disruptive selection is strengthened when species are dietary generalists, and wider diets also support top predators with larger body size. Of course, factors for initial diversification may be different from those that influence eventual diversity maintenance, similar to the case of community succession where pioneer species are often have distinct traits from climax species at later succession stages.

Coevolutionary networks provide an ideal model of complex adaptive systems. In this system, it is important to choose adaptively with whom to interact (habitat and diet selection) or to avoid (anti-predation strategies) (Zhang et al. 2011). Such interactions are often assortative as modelled by the function of α and γ used in above models. Assortative mating is important for evolutionary branching in sexual populations, while assortative cross-trophic interactions are essential for adaptive

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diversification in coevolutionary systems. Such preferential interactions could simply arise from optimal or adaptive foraging where species aim to maximize their energy intake rate (Zhang and Hui 2014), while being undermined by others during their maximization. This is a grand multiplayer game. To survive in such a game, species often have to have multiple contingency plans with which to handle ecological or evolutionary selection pressures. Ecologically, species can adjust the extent and structure of their geographical range, or simply shifting its range (Roura-Pascual et al. 2011), forming different aggregation patterns of biodiversity (e.g. Hui and McGeoch 2014). They can also invoke different population dynamic strategies to release the pressure, e.g. population cycles (Ramanantoanina et al. 2011; Zhang and Hui 2011). For evolutionary pressures, species can modify their functional traits convergently or divergently (e.g. Berthouly-Salazar et al. 2012, 2013). They can change their morphology, phenology, tolerance, performance and plasticity, which are reinforced by heritable genotypes, leading to diverse evolutionary trajectories.

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